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Revision of the *Polynema dikobraz* species-group with description of a remarkable new species from South Africa (Hymenoptera, Chalcidoidea, Mymaridae)

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Abstract

A new Afrotropical species of *Polynema* Haliday, 1833 (Hymenoptera: Mymaridae), *Polynema* (*Polynema*) *sagittaria* van Noort & Triapitsyn, **sp. n.**, is described and illustrated based on specimens collected in the Cape Floral region in south-western South Africa. This species is morphologically closely related to the recently described *Polynema* (*Polynema*) *dikobraz* Triapitsyn, 2017 from Madagascar, both species possessing enlarged spine-like microtrichia on the fore wing disc that are unique among all the known world fairyflies. This new species belongs to the informal *dikobraz* species-group of the nominate subgenus of *Polynema*, which previously was only known from Madagascar. In addition, *P. sagittaria* has the ovipositor extending ventrally under the mesosoma to well in front of the head, in a bow-like curve, and housed in a narrow, anterior elongation of the metasoma, the basal sac. Occurrence and possible significance of such a bizarre ovipositor in other Mymaridae is discussed. All images and online keys are available on www.waspweb.org

Keywords

Africa, Afrotropical region, identification key, ovipositor, *Polynema dikobraz* species-group, taxonomy

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Introduction

The Afrotropical mymarid fauna is poorly known, with only 21 species of the extremely diverse and species-rich genus, *Polynema* Haliday, 1833, described from the region. Most of these are known from only two countries: Democratic Republic of the Congo, as a result of the Belgian taxonomist H. R. Debauche's (1949) description of 11 species of *Polynema*, under the name *Maidliella* Soyka, 1946, a synonym of *Polynema* (the single species he described as a *Polynema* is now in *Stephanodes* Enock, 1909), and Girault's (1917a, 1917b) description of 5 species from Tanzania. However, at least two of the species described by Debauche do not belong in *Polynema* (Triapitsyn and Aquino 2010), and the identity of Girault's species will need to be verified, based on a study of their type specimens. Three additional species are also known from Democratic Republic of the Congo, Senegal, and South Africa (Annecke and Doutt 1961, Ghesquière 1942, Risbec 1951). Triapitsyn (2017) described a remarkable new species with highly modified wing setation, *Polynema* (*Polynema*) *dikobraz* Triapitsyn, 2017, from Madagascar and placed it in the informal *dikobraz* species-group. This species has unique, enlarged spine-like microtrichia on the fore wing disc.

As part of a comprehensive, ongoing 26 year inventory survey of Afrotropical Hymenoptera by the senior author, four females of a continental African species belonging to the *P. dikobraz* species-group were collected in the Western Cape Province of South Africa. A fifth female from the same region was located in the CNCI collection in Ottawa, Canada. They possess the same remarkable fore wing microtrichia and also have a unique, anteriorly projecting ovipositor, the first described for *Polynema*. Because this is the first continental African species in a unique species-group of *Polynema* and the need to provide a taxon name for the extracted DNA sequence, we have undertaken a revision of this small species-group. We also discuss the ovipositor structure and place it in context of the evolution of other modes of hymenopteran ovipositor adaptation. An identification key is provided to the species of the *Polynema* (*Polynema*) *dikobraz* group. Online Lucid identification keys and all images are available at www.waspweb.org.

Materials and methods

Ethanol-preserved specimens were either dried using the HMDS procedure following Heraty and Hawks (1998), or using a Critical Point Dryer (Leica EM CPD300). For slide preparation the specimens were cleared in 10% KOH solution prior to dehydration through an ethanol series, final dehydration in Euparal and dissection and mounting in Canada balsam on a glass slide under coverslips.

Images were acquired at SAMC with a Leica LAS 4.9 imaging system, comprising a Leica Z16 microscope (using either a 2× or 5× objective) with a Leica DFC450 Camera and 0.63× video objective attached. The imaging process, using an automated Z-stepper, was managed using the Leica Application Suite V 4.9 software installed on a desktop computer. Diffused lighting was achieved using a Leica LED5000 HDI dome. All images presented in this paper, as well as supplementary images, are available at www.waspweb.org

Morphological terminology follows Heraty et al. (2013), Triapitsyn (2017) and the Hymenoptera Anatomy Ontology (HAO: http://portal.hymao.org) (Seltmann et al. 2012). Measurements are given in micrometers.

Codens of depositories of specimens follow Arnett et al. (1993):

CASC California Academy of Sciences, San Francisco, California, USA (Curator: Brian L. Fisher)

CNCI Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Canada (Curator: Sophie Cardinal)

SAMC Iziko South African Museum, Cape Town, South Africa (Curator: Simon van Noort)

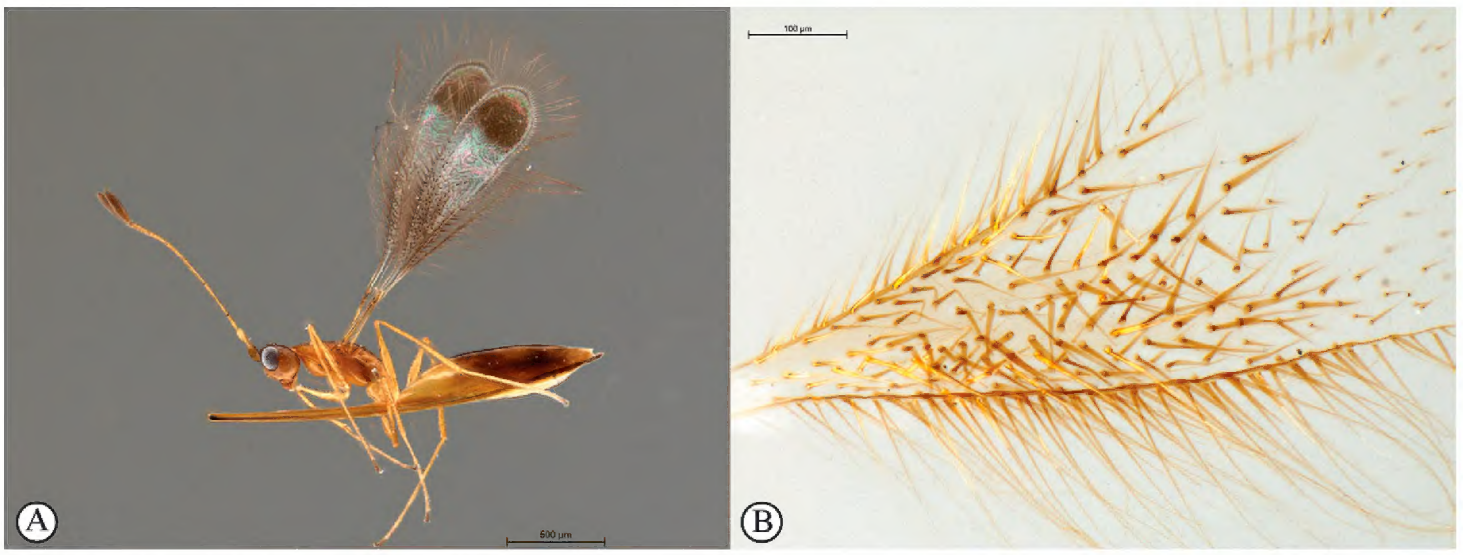
UCRC Entomology Research Museum, Department of Entomology, University of California, Riverside, California, USA (Curator: Serguei V. Triapitsyn)

Results

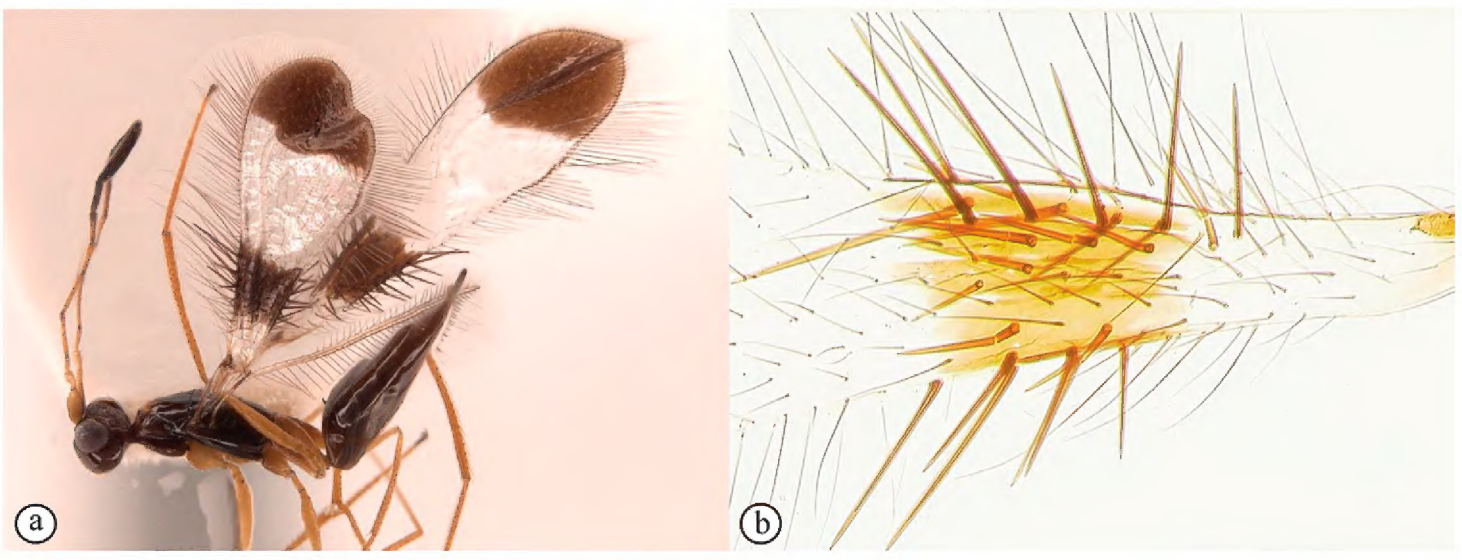
Key to species of the *Polynema* (*Polynema*) *dikobraz* species-group

1 Fore wing with enlarged spine-like microtrichia on basal third of disc (A, B) (*Polynema* (*Polynema*) *dikobraz* species-group) **2**

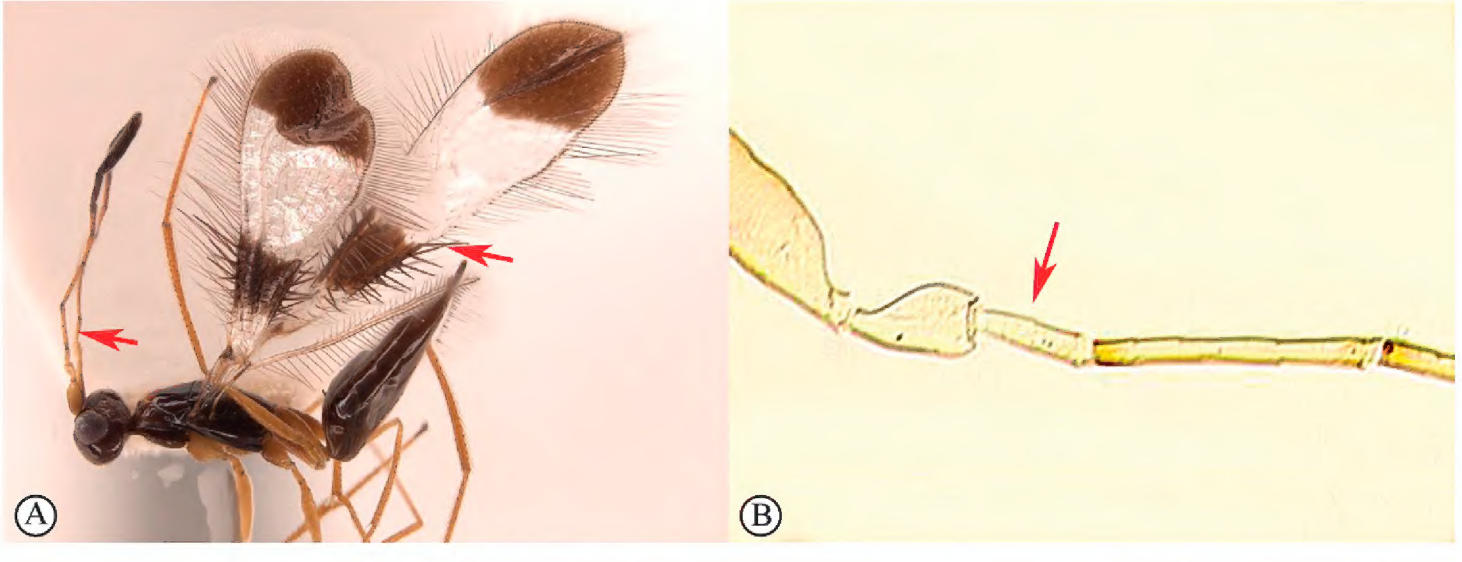
– Fore wing disc with microtrichia normal, evenly-sized across disc (a, b) .... **all other *Polynema* species**



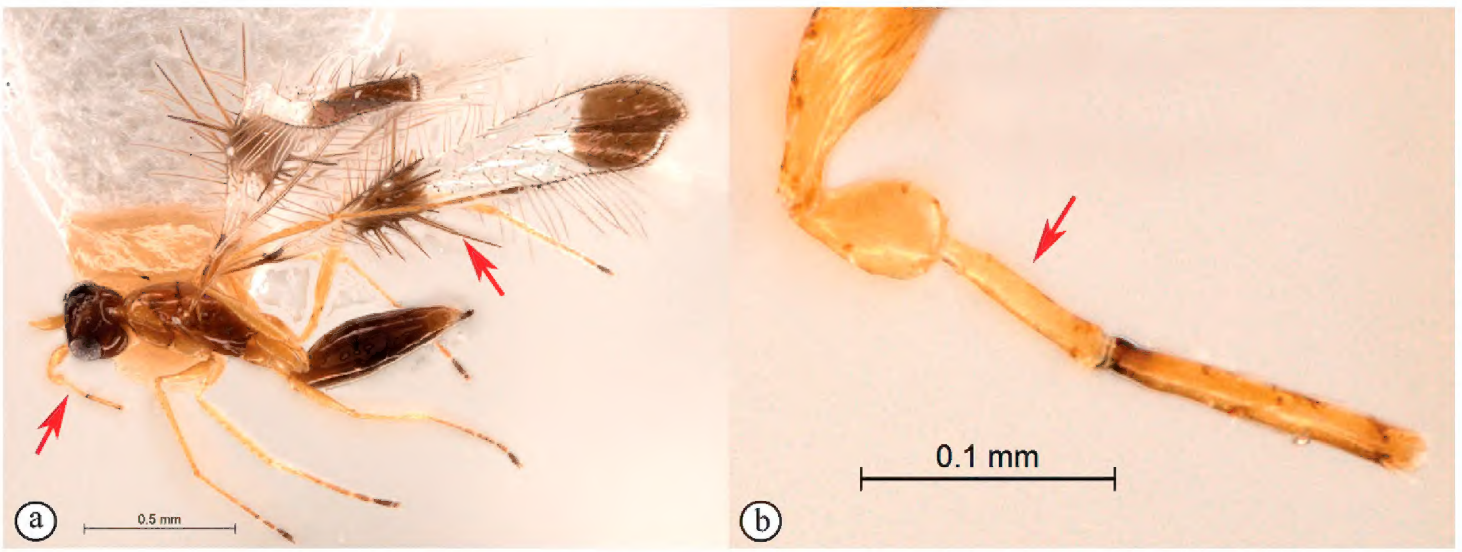
2 Ovipositor extending forward underneath the body to in front of the head (A); modified fore wing disc microtrichia numerous and shorter (B)..... .....***P. sagittaria* sp. n.**



– Ovipositor normal, not extending forward underneath the body (a); modified fore wing disc microtrichia less numerous and longer (b) **3**



3 Longest modified wing spine marginally longer than wing width at point of spine attachment (A); mesosoma dark brown (A); first flagellar antennal segment equivalent to pedicel length (A, B).....***P. dikobraz* Triapitsyn**



– Longest modified wing spine far longer than wing width at point of spine attachment (a); mesosoma mostly light brown with some dark brown areas (a); first flagellar antennal segment longer than pedicel length (a, b) ....***Polynema* species near *P. dikobraz***

Polynema (*Polynema*) *dikobraz* species-group

Diagnosis. The *Polynema dikobraz* species-group is characterized by the possession of modified microtrichia on the fore wing disc (Triapitsyn 2017).

Affinities. This species-group belongs to the nominate subgenus of *Polynema* based on absence of pits near the toruli; an "open" prosternum; a characteristic short marginal vein on the fore wing; petiole attached posteriorly to the gastral tergum; and male genitalia with digital hooks (Triapitsyn and Fidalgo 2006, Triapitsyn 2017).

Distribution. Madagascar, South Africa.

Habitat. Associated with montane rainforest and fynbos.

Polynema (*Polynema*) *dikobraz* Triapitsyn, 2017

Material. *Holotype* ♀ examined, dissected under 4 coverslips on slide and almost complete (lacking a radicle of one antenna): MADAGASCAR, Prov. D'Antanarivo 3 km 41°NE Andranomay, 11.5 km 147° SSE Anjozorobe, el. 1300 m 5–3.xii.2000, 18°28'24"S, 47°57'36"E, Fisher, Griswold et al. California Academy of Sciences Montane rainforest, MT, coll code BLF2372, CAS LOT # 005501, Mounted at UCR/ERM by V.V. Berezovskiy 2011 in Canada balsam, *Polynema* (*Polynema*) *dikobraz* Triapitsyn HOLOTYPE ♀, Det. by S.V. Triapitsyn 2011 (CASC).

Diagnosis. Morphologically similar to the newly described species, *P. sagittaria* sp. n., both species having enlarged spine-like microtrichia. *Polynema dikobraz*, however, has a normal ovipositor, and is closely related to an undescribed species, from which it can be separated by the length of the modified wing spine and relative length of the first antennal flagellar segment.

Affinities. Based on the hypothesized morphological synapomorphy of modified (long, thick) microtrichia on the fore wing disc, *P. dikobraz* is related to *P. sagittaria* **sp. n.**, but has far fewer, and longer modified wing disc microtrichia. This species also has a normal ovipositor as in other members of *Polynema*, as opposed to the highly modified ovipositor of *P. sagittaria*.

Distribution. Madagascar.

Habitat. Montane rainforest.

Polynema (*Polynema*) *sagittaria* van Noort & Triapitsyn, sp. n.

http://zoobank.org/BF62E578-DB4E-4632-9AB2-A12FE7E10AF1

Figs 1A–F, 2A–F, 3A–F, 4A–D

Material. *Holotype* ♀ (deposited in SAMC), point mounted: SOUTH AFRICA, Western Cape, Cederberg, Sawadee Farm, 32°19.92'S, 18°59.24'E, 24–28.ix.2003, S. van Noort, Malaise trap, CE03-M01, Dry Mountain Fynbos, 380 m, SAM-HYM-P086324, imaged WaspWeb, LAS 4.9, SAMC 2017. *Paratypes*. SOUTH AFRICA, Western Cape: same data as holotype, except for collecting event number: CE03-M05, and catalogue number: SAM-HYM-P086325, imaged WaspWeb, LAS 4.9, SAMC 2017 (1 ♀ on slide, SAMC); Banghoek Valley, Dwarsriviershoek Farm, 33°56.23'S, 18°57.71'E, 410 m, 22.x–27.xi.2013, S. van Noort, Malaise trap, Mesic Mountain Fynbos, BH12-FYN3-M14, SAM-HYM-P084138 (1 ♀ on slide, SAMC) [specimen lacks both hind wings; DNA was extracted using a non-destructive method, John M. Heraty's Laboratory molecular voucher D6195]; Kogelberg Nature Reserve, 34°16.48'S, 19°01.03'E, 16.x–16.xi.1999, S. van Noort, Malaise trap, K098-M44, Mesic Mountain Fynbos, last burnt c. 1988, SAM-HYM-P082695 (1 ♀ on point, SAMC); 10 km S of Citrusdal, Kornlandskloof [S32°40', E19°02], 7–9.x.1994, meadow at stand of *Herrea blanda*, M. Sodelund, MT (1 ♀ on point, CNCI).

Etymology. The species epithet "*sagittaria*" is Latin for armed with bow, with reference to the bowed ovipositor sheaths. Noun in apposition.

Diagnosis. The highly modified ovipositor immediately distinguishes this species from all other described *Polynema* species in Africa. Morphologically similar to the recently described species, *P. dikobraz* from Madagascar, and the second undescribed Madagascan species, all three species having similar modified fore wing microtrichia.

Affinities. Based on the putative morphological synapomorphy of modified microtrichia on the fore wing disc, *P. sagittaria* is clearly related to *P. dikobraz*, but has more numerous, shorter modified wing disc microtrichia than in *P. dikobraz*. The extensive external ovipositor housing is an obvious distinction within the *P. dikobraz* species-group, but this is likely to be a character state that has evolved independently in a number of mymarid genera (see discussion).

Distribution. South Africa. Only known from the Western Cape Province.

Habitat. Mountain fynbos, a vegetation type specific to the Cape Floral region.

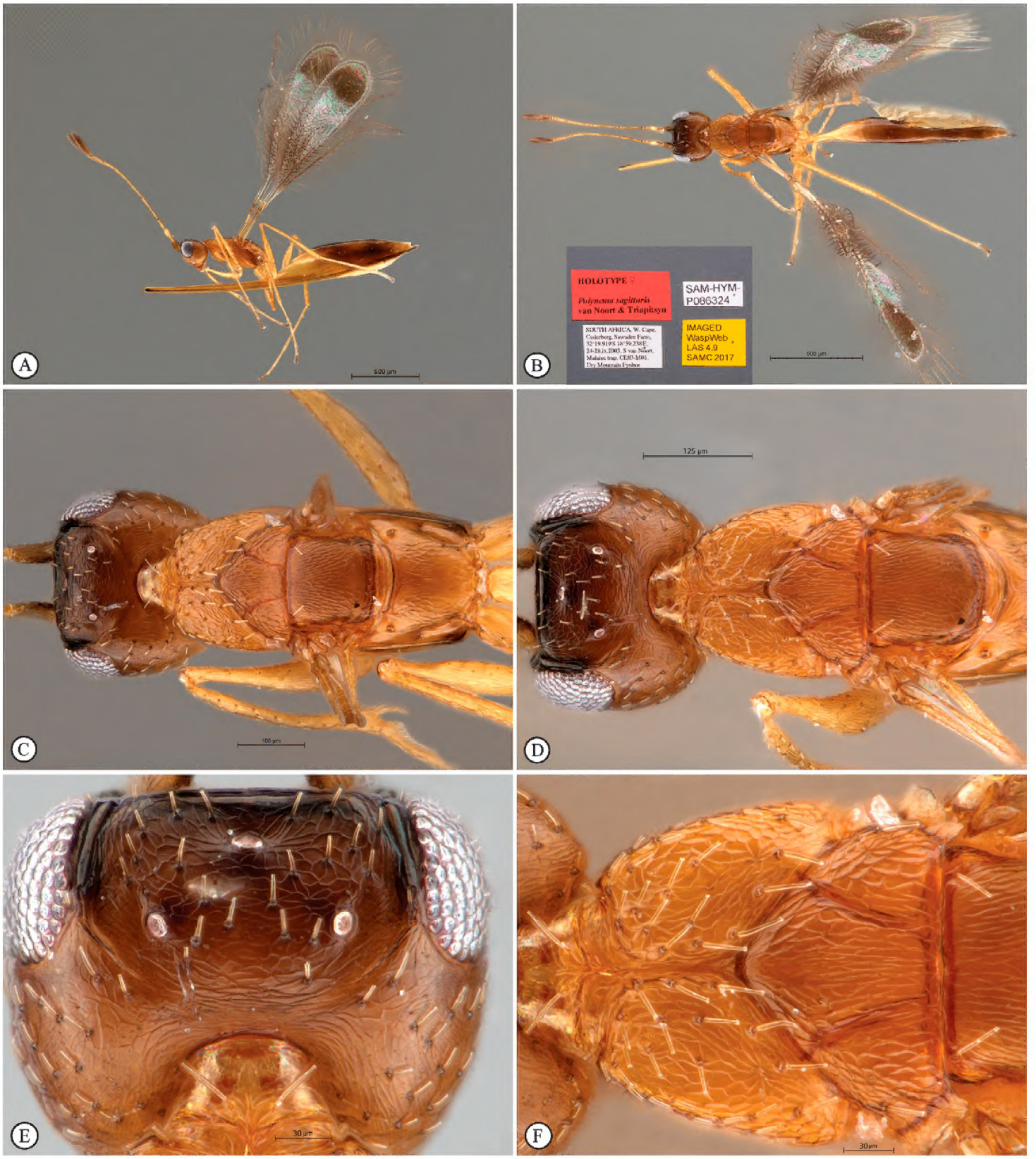


Figure 1. *Polynema sagittaria* Holotype female. **A** Habitus, lateral view **B** Habitus, dorsal view (inset: data labels) **C** Head and mesosoma, dorsal view **D** Head and mesosoma, anterior-dorsal view **E** Head, vertex **F** Pronotum and mesoscutum, dorsal view.

Description of female holotype. *Size and colour*. Total length of body, with head in prognathous position, 1700 µm. Head 205; mesosoma 511; petiole 114; metasoma 1140; ovipositor 2110 folded, 3800 total length (unfolded). Antenna: radicle 18; rest of scape 96; pedicel 91; F1 92; F2 204; F3 173; F4 115; F5 97; F6 94; clava 204. Fore wing 1670: 340; longest marginal seta 517; longest discal (spine-like) seta 117. Hind wing 1260: 23; longest marginal seta 267. Habitus (Fig. 1A, B). Head dark brown

Figure 2. *Polynema sagittaria* Holotype female. **A** Body, lateral view **B** Head, anterior view **C** Antennae, lateral view **D** Antennae, dorsal view **E** Antennal clavae, dorsal view **F** Wings, dorsal view.

to black on vertex, face and mesosoma yellowish-brown, pedicel and anterior third of metasoma yellowish, rest of metasoma dark brown; scape dark brown, pedicel and F1–F6 yellowish, clava dark brown; legs yellowish.

Head (Figs 1E, 2B, 3A). Mandible 3-dentate. Antenna (Figs 2C–E): scape coriaceous, 2 × as long as wide in lateral view (excluding a short radicle); pedicel as long as F1; F2 the longest funicular segment, F3 longer than the following funicular segments, F4 a little longer than F5, the latter slightly longer than F6, F6 with one mps; clava long, 4 × as long as wide, with 4 mps (3 apical and 1 subapical).

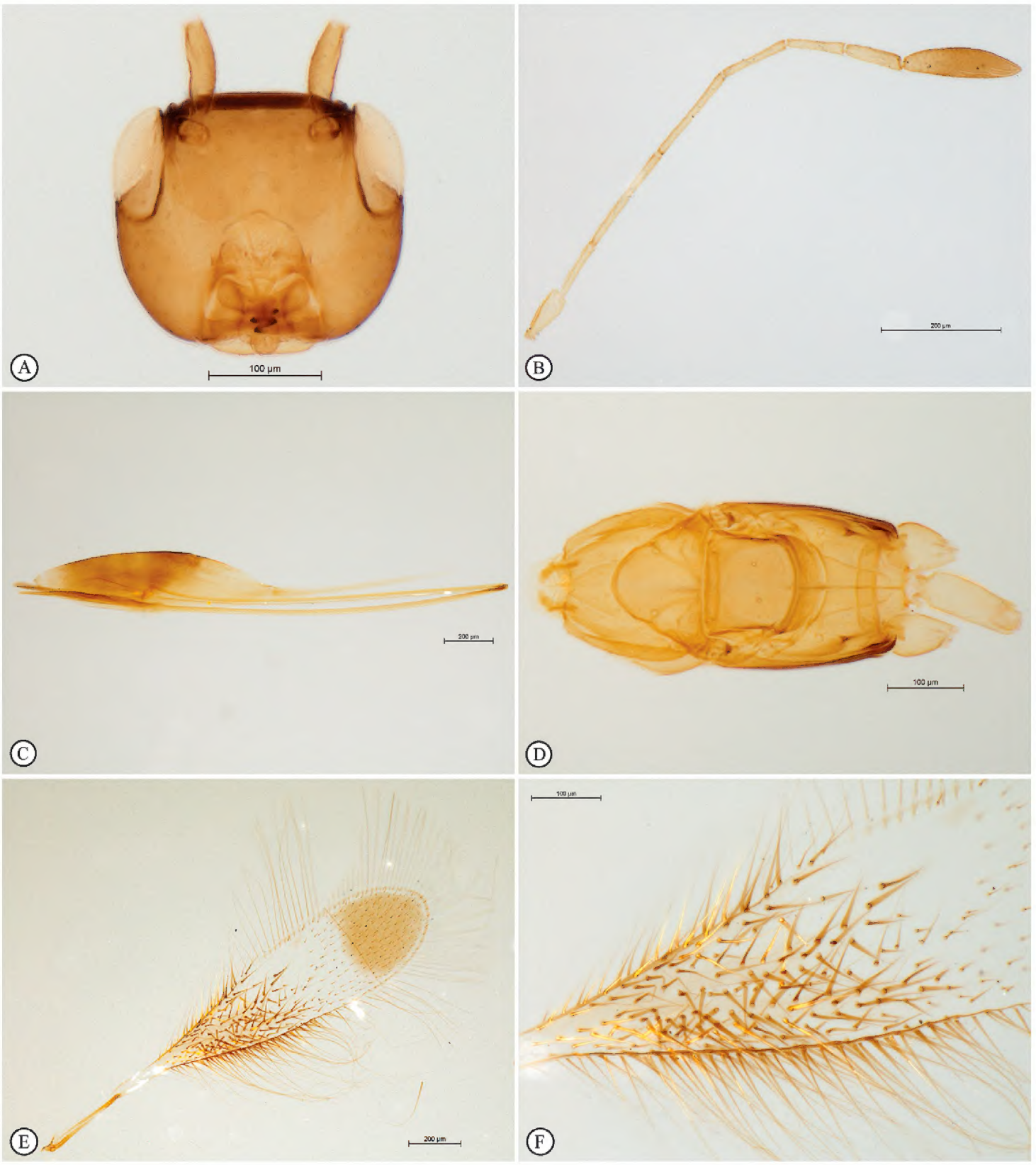


Figure 3. *Polynema sagittaria* Paratype female, slide-mounted. **A** Head, anterior view **B** Antenna, lateral view **C** Metasoma, lateral view **D** Mesosoma and petiole, dorsal view **E** Fore wing, dorsal view **F** Fore wing discal microtrichia, dorsal view.

Mesosoma (Figs 1C–D, 1F, 3D). Coriaceous. Pronotum mediolongitudinally divided, with numerous stout, truncate setae, collar with two strong truncate setae. Mesoscutum 1.8 × as wide as long, 0.75 × scutellar length. Axilla with 1 strong truncate seta (30 µm). Scutellum with a row of tiny, indistinct foveae on frenal line; with two anterior truncate setae. Propodeum smooth, with a truncate seta each side of the midline. Fore wing (Figure 2F) 4.9 × as long as wide; submarginal vein without seta, marginal vein with 1 dorsal seta; longest marginal seta 0.785 × maximum width of wing; disc with a

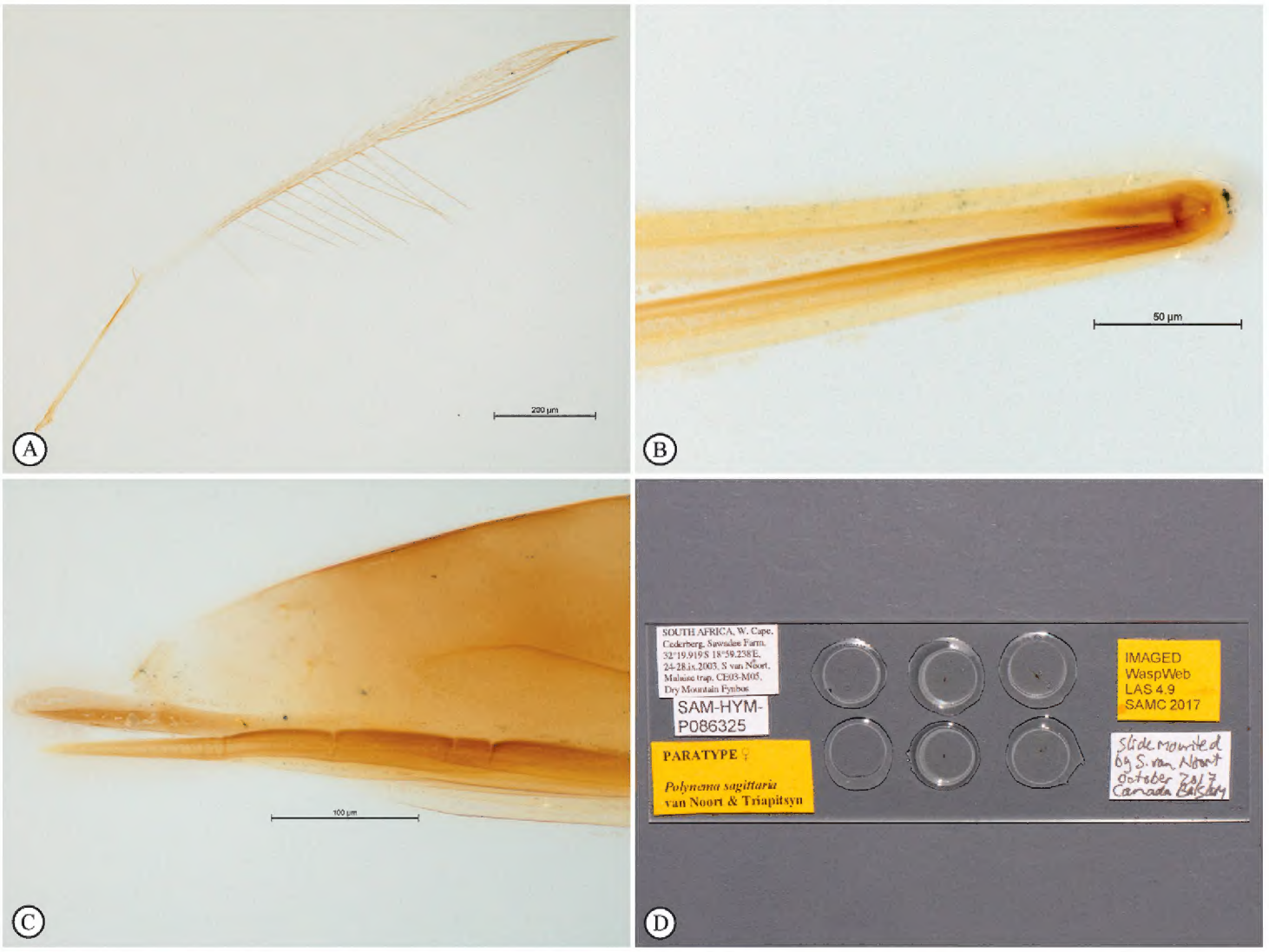


Figure 4. *Polynema sagittaria* Paratype female, slide-mounted. **A** Hind wing, dorsal view **B** Ovipositor distal flexion, lateral view **C** Ovipositor valves with terminal annuli and three dorsal notches on dorsal valve, sheaths and terminal metasomal segments, lateral view **D** Slide detail.

distinct apical brown patch in close apposition to wing margin, occupying approximately a third of wing disc length; brownish areas in apical third of disc among spine-like microtrichia; disc setose throughout (apical two thirds of disc with normal microtrichia), with 130–140 very long, dark brown, strongly enlarged spine-like modified microtrichia (Figs 1A, 2F, 3E, 3F) on proximal brown infuscation area on wing disc. Hind wing (Figs 2F, 4A) 54.8 × as long as wide; apex of venation with a short, thickened seta; disc slightly infumate, longest marginal seta 11.6 × maximum width of wing. All coxae smooth.

Metasoma (Figs 2A, 3C). Petiole smooth, approximately 3 × as long as wide, slightly longer than metacoxa; ovipositor extending anteriorly in metasomal sac between the legs, 1.3 × further forward than head length; doubled back on itself in a bow-like fashion, with complex fold at anterior extremity (Figure 4B); only slightly extending beyond the metasomal apex by 0.05 × metasomal length, 1.24 × length of body in folded position (Figure 2A), 2.23 × length of body if totally extended in unfolded position; ovipositor valve with 10 closely-spaced, indistinct, terminal annuli; pre-terminally with three unevenly spaced dorsal notches (Figure 4C).

Variation. Body length 1.45–1.68 mm; ovipositor (folded) length 1.93–2.00 mm in the paratype specimens.

Male. Unknown.

Polynema species near to *P. dikobraz*

Material. MADAGASCAR, Diana Region, Amber Mountain National Park, 12°31'13"S, 49°10'45"E, 1125 m, 29.i–11.ii.2001, R. Harin'Hala [1 ♀, CASC].

Notes. An additional species that is morphologically similar to *P. dikobraz* is known from Madagascar (Triapitsyn 2017). We refrain from describing this species here until further specimens are obtained. The single known specimen is damaged. We have, however, included this taxon in the identification key to facilitate recognition of the species.

Discussion

For female wasps to successfully access and oviposit into hosts living within substrates, this either requires an elongate ovipositor, or an ability on the part of the female wasp to navigate through the substrate to reach the host for direct oviposition. The latter option appears to have driven evolution of various types of facial protrusions, which at least in the case of the ichneumonid genus *Genaemirum* Heinrich, 1936, has led to the hypothesis that the highly modified spade-like protrusions of the clypeus and genae are used in a shoveling manner to facilitate negotiation of the frass-filled tunnels created by the wood-boring host moth caterpillar, in order to reach the pupae for oviposition (Rousse et al. 2016). A number of species in other parasitoid wasp groups (Chalcidoidea, Diaprioidea, Figitidae, Platygastroidea, Protrotrupidae) also have facial protrusions, for which a functional hypothesis has yet to be postulated (Nielsen and Buffington 2011, Buffington and Copeland 2015, Buffington et al. in press). In terms of evolution of an elongate external ovipositor, logically it would be expected that natural selection will drive evolutionary adaptation to an optimal morphological configuration to attain a functional balance between successful host access for oviposition, and efficient flight without hindrance by a cumbersome ovipositor.

Across the Hymenoptera a number of different morphological metasomal configurations have evolved in response to this evolutionary driver of host reaching ability, with the elongate ovipositor being either housed within the metasoma in various configurations, or encased in elongated external ovipositor sheaths. Basal Hymenoptera have the ovipositor contained within the metasoma (Quicke et al. 1992, 1999, Vilhelmsen 2000, Vilhelmsen et al. 2001, Vilhelmsen and Turrisi 2011), and evolution of external ovipositor sheaths housing the valves have enabled many of the higher wasp lineages to evolve extremely long ovipositors allowing females to access hosts concealed much deeper within substrates (Quicke 2015, Vilhelmsen 2003). Life history mode, i.e., whether the strategy is one of ectoparasitism or endoparasitism, is a further underlying driver that will influence evolution of ovipositor morphology (Quicke and Fitton 1995, Belshaw et al. 2003). In concert with ovipositor elongation, evolution of the wasp "waist" has allowed for maneuvering of the metasoma to permit vertical drilling by the ovipositor (Vilhelmsen et al. 2010; Vilhelmsen 2013). For example,

ichneumonoid and other wasp taxa with elongate ovipositor sheaths need to place the tip of the ovipositor at the oviposition site and to then walk backwards, which raises the metasoma and sheaths allowing for the vertical positioning of the ovipositor prior to commencement of drilling (Quicke et al. 1994, Quicke 2015). Chalcidoid wasps in a number of families, particularly the non-pollinating fig wasps have evolved a similar oviposition strategy and a number of pteromalid lineages associated with figs have evolved various adaptations of the metasomal terminal terga to lengthen the functional ovipositor (Wiebes 1966, Copland et al. 1973, Ulenberg 1985). It seems likely that *P. sagittaria* will need to employ a similar strategy of placing the ovipositor tip on the selected drilling site followed by backwards walking and simultaneous raising of the metasoma to effectively deploy the ovipositor, although mode of drilling and disengagement of the valves from the ovipositor sheaths will probably be different, given that the ovipositor sheaths are folded forwards underneath the body. Direct observation of ovipositing females is required to elucidate the precise mechanism, though this is a high expectation given the rarity of the species.

A number of parasitoid wasp taxa, particularly in the Platygastridae *sensu lato* (Platygastroidea), have evolved modifications of various parts of the metasoma to accommodate internal housing of the elongate ovipositor valves, in lieu of long external ovipositor sheaths (Austin and Field 1997). In a number of scelionine genera these modifications may include a telescopic ovipositor system, where the ovipositor is invaginated entirely into the body cavity, but can be extended by over three times its actual length via intersegmental membrane elongation, operated by hydrostatic pressure; or alternatively, may comprise an ovipositor system that is extended and retracted by antagonistic muscles (Austin and Field 1997, Field and Austin 1994). In various platygastrid genera, housing of the ovipositor is accommodated in an extension of the first metasomal tergite into variable forms ranging from a bump to elongate horn-like processes extending forwards above the mesosoma (Austin and Field 1997). The unusual extension of the ovipositor forwards under the body and head (in *P. sagittaria* and other mymarid genera), is a further example of evolutionary adaptation of metasomal morphology to house an elongate ovipositor. The ovipositor appears to be housed in a membranous anterior extension of a metasomal sternite. This is also evident in species of *Anaphes* Haliday, 1833 where this anterior extension of a metasomal sternite or "sac of gaster" was postulated to consist mainly of gs6 (Huber and Thuróczy 2018). Not surprisingly the configuration of the rami and associated musculature in *P. sagittaria* (Fig. 3C) diverges somewhat from the standard configuration for Mymaridae (King and Copland 1969), a structural necessity allowing for the ovipositor to initially project directly forwards instead of immediately curving ventrally in order to extend in a posterior direction. An intermediate evolutionary configuration is evident in species of *Anaphes* where the ovipositor has begun to extend forwards, housed in a broader membranous anterior extension of metasomal sternite 6 "gs6" (Huber and Thuróczy 2018), providing evidence of the evolutionary process leading to the substantial forward elongation of the ovipositor in *P. sagittaria*. The Chalcidoidea have asymmetric and overlapping halves of the upper ovipositor valve, including thickenings of the

upper and lower valve walls, purported apomorphies defining the superfamily, but with exclusion of Mymaridae (Quicke et al. 1994). The upper valve of Mymaridae in cross section is symmetric and relatively simple, although its ventral wall is also thickened (Quicke et al. 1994). This sister-group relationship of Mymaridae to the remaining Chalcidoidea was supported by the molecular and morphological phylogenetic analyses of the Chalcidoidea conducted by Heraty et al. (2013). Elucidating the detailed structure and function of the ovipositor's morphological configuration in *P. sagittaria* requires further investigation using techniques such as thin-sectioning or CT scanning.

Among other world *Polynema* species, the ovipositor of *P. sagittaria* is unique in the extreme degree of its protrusion forward beyond its head, but a few undescribed species of *Polynema*, such as a *Polynema* species from Tanzania (one female in UCRC) and Nepal (females in CNCI), also possess such a feature, although their ovipositor is relatively shorter than in *P. sagittaria* and does not project forward beyond the head, but does reach anteriorly almost to, or even beyond the anterior margin of the mesosoma. In Mymaridae other than *Polynema*, an ovipositor similar to that in *P. sagittaria* also occurs in several other genera, such as *Gahanopsis* Ogloblin, 1946, *Gastrogonatocerus* Ogloblin, 1935, *Lymaenon* Walker, 1846 (mainly in some Australasian species), and *Neotriadomerus* Huber, 2017 (Huber 2015, 2017), and *Paranaphoidea* Girault, 1913 (Huber and Triapitsyn 2017). Thus, in Mymaridae, at least two evolutionary strategies of developing very long ovipositors can be noted. First, it is a simple lengthening of the ovipositor (and the ovipositor sheaths) beyond the posterior apex of the metasoma, with or without a large basal loop within the metasoma, but without the anterior protrusion. This happens multiple times in different, often unrelated, lineages within the family, such as in some Afrotropical species of the subgenus *Anagrella* Bakkendorf, 1962 of *Anagrus* Haliday, 1833 (Triapitsyn 2015), *Kalopolynema* Ogloblin, 1960 (Triapitsyn and Berezovskiy 2002), and *Omyomymar* Schauff, 1983 (Schauff 1983). The other strategy, which is found in *P. sagittaria* as well as in some members of Gonatocerini mentioned above and also in some *Australomymar* Girault, 1929 (Noyes and Valentine 1989) and *Paranaphoidea* (Huber and Triapitsyn 2017), the ovipositor strongly projects forward under the mesosoma, sometimes beyond the head. Such very long ovipositors are needed in the situations where host eggs are concealed within plant tissue, like the aerenchyma of some aquatic plants, which is the apparent case in *Kalopolynema* species having a large basal loop within the metasoma (Triapitsyn and Berezovskiy 2002), or within some other substrate or crevice. For instance, the Neotropical species *Gastrogonatocerus membraciphagus* (Ogloblin, 1935) has a similar ovipositor to that of *P. sagittaria* although it is relatively shorter and not projecting beyond the head. Paul Bertner (personal communication) recently observed a female of *G. membraciphagus* in Ecuador examining (Fig. 5A–B) an egg mass of a treehopper (Hemiptera, Membracidae), similar in appearance to a *Bolbonota* sp. which is a known host of this fairyfly species (Triapitsyn et al. 2010), and subsequently to oviposit into the egg mass (Figure 5C). The long ovipositor is clearly seen to be used to penetrate the thick foam covering the eggs of the treehopper (Figure 5C).

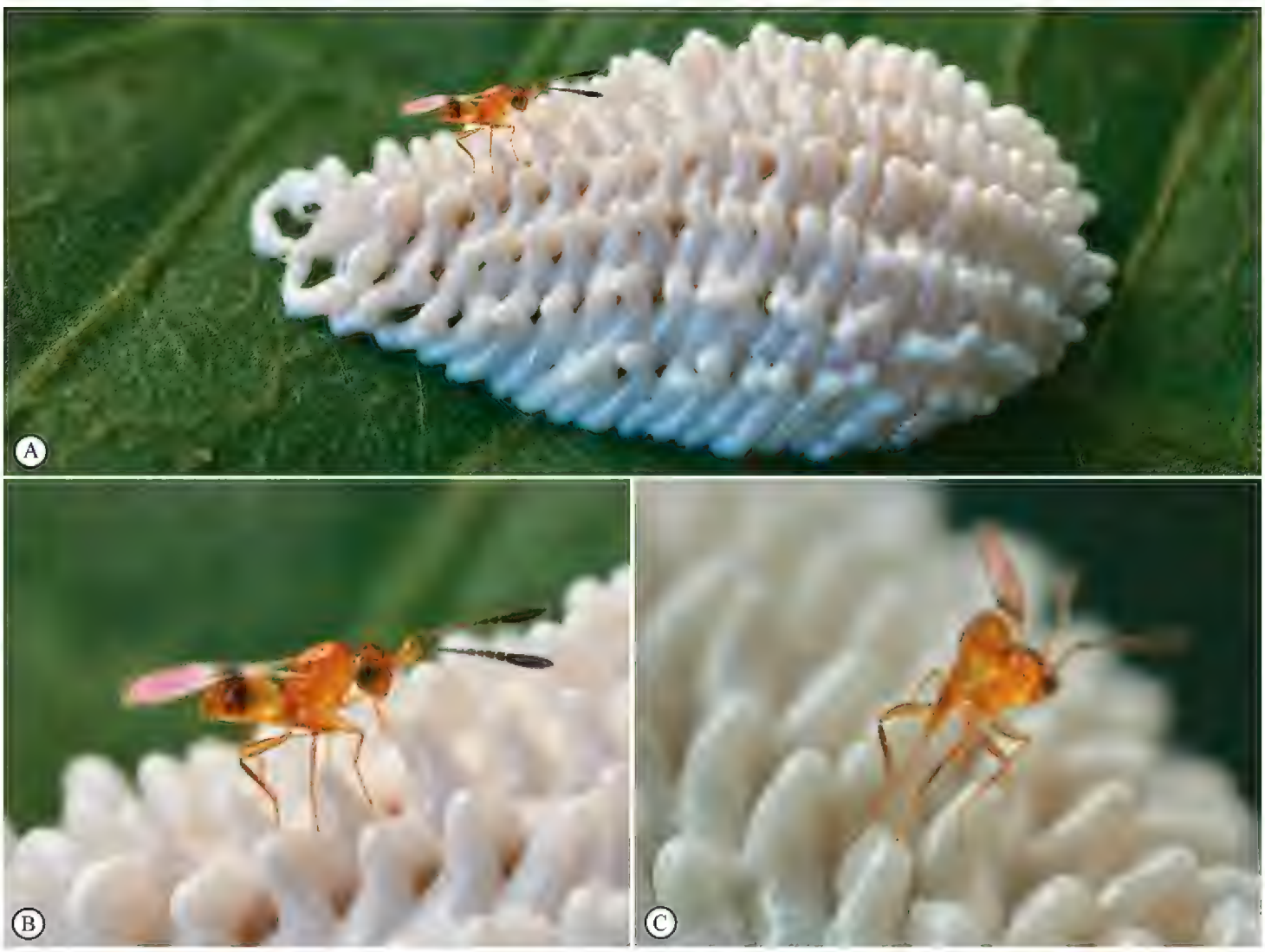


Figure 5. *Gastrogonatocerus membraciphagus*. The photographs (courtesy of Paul Bertner) were taken at the Sani Lodge Prinicipal, Río Napo, Yasuní, Orellana, Ecuador, in January 2018. **A** Female (in lateral vew) on an egg mass of a treehopper (Membracidae), similar in appearance to a *Bolbonota* sp. **B** Same female (in close-up) **C** Same female (in rear view) ovipositing in that egg mass.

In all likelihood the long ovipositor of *P. sagittaria* is a similar adaptation to reach host eggs concealed within a secondary substrate. Based on the presence of annuli at the tip of the ovipositor, which are an adaption to drill through hard surfaces (Ernst et al. 2013, Quicke et al. 1999, Le Ralec et al. 1996), we hypothesize that the host eggs themselves, or the substrate within which they are concealed is hard.

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References

Annecke DP, Doutt RL (1961) The genera of the Mymaridae (Hymenoptera: Chalcidoidea). Entomology Memoirs of the Department of Agricultural Technical Services of the Republic of South Africa 5: 1–71.

Arnett Jr RH, Samuelson GA, Nishida GM (1993) The Insect and Spider Collections of the World (Second Edition) Flora and Fauna Handbook No. 11. Sandhill Crane Press, Gainesville, 310 pp.

Austin AD, Field SA (1997) The ovipositor system of scelionid and platygastrid wasps (Hymenoptera: Platygastroidea): comparative morphology and phylogenetic implications. Invertebrate Systematics 11: 1–87. https://doi.org/10.1071/IT95048

Belshaw R, Grafen A, Quicke DLJ (2003) Inferring life history from ovipositor morphology in parasitoid wasps using phylogenetic regression and discriminant analysis, Zoological Journal of the Linnean Society 139: 213–228. https://doi.org/10.1046/j.1096-3642.2003.00078.x

Buffington ML, Copeland R (2015) *Muhaka icipeins*, an enigmatic new genus and species of Kleidotomini (Hymenoptera: Figitidae: Eucoilinae) from an East African coastal forest. Journal of Natural History 49: 2597–2607. https://doi.org/10.1080/00222933.2015.1042411

Buffington ML, Copeland R, van Noort S (in press) Revision of *Afroserphus* Masner (Hymenoptera: Proctotrupidae) with the description of two new species. Proceedings of the Entomological Society of Washington.

Copland MJW, King PE, Hill DS (1973) The structure of the female reproductive system in the Agaonidae (Chalcidoidea, Hymenoptera). Journal of Entomology Series A, General Entomology 48(1): 25–35. https://doi.org/10.1111/j.1365-3032.1973.tb00029.x

Debauche HR (1949) Mymaridae (Hymenoptera, Chalcidoidea). Exploration du Parc National Albert, Mission G.F. de Witte 49: 1–105.

Ernst A, Miko I, Deans A (2013) Morphology and function of the ovipositor mechanism in Ceraphronoidea (Hymenoptera, Apocrita). Journal of Hymenoptera Research 33: 25–61. https://doi.org/10.3897/jhr.33.5204

Field SA, Austin AD (1994) Anatomy and mechanics of the telescopic ovipositor system of *Scelio* Latreille (Hymenoptera: Scelionidae) and related genera. International Journal of Insect Morphology and Embryology 23: 135–158. https://doi.org/10.1016/0020-7322(94)90007-8

Ghesquière J (1942) Contribution à l'étude des Hyménoptères du Congo Belge. IX. Revue de Zoologie et de Botanique Africaines 36: 317–328.

Girault AA (1917a) Some new Mymaridae and a new *Signiphora* in the collections of the Zoological Museum, Berlin. (continued) Societas Entomologica [Frankfurt] 32(4): 17.

Girault AA (1917b) Some new Mymaridae and a new *Signiphora* in the collections of the Zoological Museum, Berlin. (continued) Societas Entomologica [Frankfurt] 32(5): 19–20.

Heraty JM, Burks RA, Cruaud A, Gibson GAP, Liljeblad J, Munro J, Rasplus J-Y, Delvare G, Janšta P, Gumovsky A, Huber J, Woolley JB, Krogmann L, Heydon S, Polaszek A, Schmidt S, Darling DC, Gates MW, Mottern J, Murray E, Dal Molin A, Triapitsyn S, Baur H, Pinto JD, van Noort S, George J, Yoder M (2013) A phylogenetic analysis of the megad-

iverse Chalcidoidea (Hymenoptera). Cladistics 29: 466–542. http://dx.doi.org/10.1111/cla.12006

Heraty JM, Hawks D (1998) Hexamethyldisilazane – a chemical alternative for drying insects. Entomological News 109(5): 369–374.

Huber JT (2015) World reclassification of the *Gonatocerus* group of genera (Hymenoptera: Mymaridae). Zootaxa 3967(1): 1–184. https://doi.org/10.11646/zootaxa.3967.1.1

Huber JT (2017) *Eustochomorpha* Girault, *Neotriadomerus* gen.n., and *Proarescon* gen.n. (Hymenoptera, Mymaridae), early extant lineages in evolution of the family. Journal of Hymenoptera Research 57: 1–87. https://doi.org/10.3897/jhr.57.12892

Huber JT, Thuróczy C (2018) Review of *Anaphes* Haliday (Hymenoptera: Mymaridae) with key to species in Europe and a world catalogue. Zootaxa 4376(1): 1–104. https://doi.org/10.11646/zootaxa.4376.1.1

Huber JT, Triapitsyn SV (2017) Two genera of Mymaridae (Hymenoptera) new to Africa, a remarkable new species of *Anaphes* and new generic synonymy. ZooKeys 658: 39–61. https://doi.org/10.3897/zookeys.658.11569

King PE, Copland MJW (1969) The structure of the female reproductive system in the Mymaridae (Chalcidoidea: Hymenoptera). Journal of Natural History 3: 349–365. https://doi.org/10.1080/00222936900770311

Le Ralec A, Rabasse JM, Wajnberg E (1996) Comparative morphology of the ovipositor of some parasitic Hymenoptera in relation to characteristics of their hosts. The Canadian Entomologist 128: 413–433. https://doi.org/10.4039/Ent128413-3

Nielsen M, Buffington ML (2011) Redescription of *Stentorceps* Quinlan, 1984 (Hymenoptera, Figitidae), with a description of five new species. African Entomology 19: 597–613. https://doi.org/10.4001/003.019.0305

Noyes JS, Valentine EW (1989) Mymaridae (Insecta: Hymenoptera) – introduction and review of genera. Fauna of New Zealand 17: 1–95.

Quicke DLJ (2015) The Braconid and Ichneumonid Parasitoid Wasps: Biology, Systematics, Evolution and Ecology. Wiley-Blackwell, Oxford, UK, 681 pp.

Quicke DLJ, Fitton MG (1995) Ovipositor steering mechanisms in parasitic wasps of the families Gasteruptiidae and Aulacidae (Hymenoptera). Proceedings of the Royal Society of London B Biological Sciences 261: 99–103. https://doi.org/10.1098/rspb.1995.0122

Quicke DLJ, Fitton MG, Ingram S (1992) Phylogenetic implications of the structure and distribution of ovipositor valvilli in the Hymenoptera (Insecta). Journal of Natural History 26(3): 587–608. https://doi.org/10.1080/00222939200770361

Quicke DLJ, Fitton MG, Tunstead JR, Ingram SN, Gaitens PV (1994) Ovipositor structure and relationships within the Hymenoptera, with special reference to the Ichneumonoidea. Journal of Natural History 28(3): 635–682. https://doi.org/10.1080/00222939400770301

Quicke DLJ, Le Ralec A, Vilhelmsen L (1999) Ovipositor structure and function in the parasitic Hymenoptera with an exploration of new hypotheses. Atti dell'Accademia Nazionale Italiana de Entomologia 47: 197–239.

Risbec J (1951) 1. Les Chalcidoides de l'Afrique occidentale française. Mémoires de l'Institute Français d'Afrique Noire, Ifan-Dakar 13: 7–409.

Rousse P, Broad GR, van Noort S (2016) Review of the genus *Genaemirum* Heinrich (Hymenoptera, Ichneumonidae, Ichneumoninae) with interactive identification keys to species. ZooKeys 636: 77–105. https://doi.org/10.3897/zookeys.636.10216

Schauff ME (1983) A new genus of Mymaridae (Hymenoptera: Chalcidoidea) from the New World. Proceedings of the Entomological Society of Washington 85: 543–551.

Seltmann KC, Yoder MJ, Mikó I, Forshage M, Bertone MA, Agosti D, Austin AD, Balhoff JP, Borowiec ML, Brady SG, Broad GR, Brothers DJ, Burks RA, Buffington ML, Campbel HM, Dew KJ, Ernst AF, Fernández-Triana JL, Gates MW, Gibson GAP, Jennings JT, Johnson NF, Karlsson D, Kawada R, Krogmann L, Kula RR, Mullins PL, Ohl M, Rasmussen C, Ronquist F, Schulmeister S, Sharkey MJ, Talamas E, Tucker E, Vilhelmsen L, Ward PS, Wharton RA, Deans AR (2012) A hymenopterists' guide to the Hymenoptera Anatomy Ontology: utility, clarification, and future directions. Journal of Hymenoptera Research 27: 67–88. https://doi.org/10.3897/jhr.27.2961

Triapitsyn SV (2015) Taxonomy of the genus *Anagrus* Haliday (Hymenoptera: Mymaridae) of the world: an annotated key to the described species, discussion of the remaining problems, and a checklist. Acta Zoológica Lilloana 59(1/2): 3–50.

Triapitsyn SV (2017) *Polynema* (*Polynema*) *dikobraz* sp. nov., a remarkable fairyfly (Hymenoptera: Mymaridae) from Madagascar. Journal of Insect Biodiversity 5(14): 1–8. http://dx.doi.org/10.12976/jib/2017.5.14

Triapitsyn SV, Aquino DA (2010) On the occurrence of *Polynema* Haliday (*Dorypolynema* Hayat and Anis) and *Palaeoneura* Waterhouse (Hymenoptera: Mymaridae) in the New World, with description of two new species. Acta Zoológica Lilloana 54(1/2): 61–77.

Triapitsyn SV, Berezovskiy VV (2002) Revision of *Kalopolynema*, with notes on *Platypolynema* (Hymenoptera: Mymaridae). Florida Entomologist 85(4): 611–619. https://doi.org/10.1653/0015-4040(2002)085[0611:ROKWNO]2.0.CO;2

Triapitsyn SV, Fidalgo P (2006) Definition of *Doriclytus*, stat. rev. as a subgenus of *Polynema* and redescription of its type species, *P. (Doriclytus) vitripenne* (Hymenoptera: Mymaridae). Zootaxa 1362: 55–68.

Triapitsyn SV, Huber JT, Logarzo GA, Berezovskiy VV, Aquino DA (2010) Review of *Gonatocerus* (Hymenoptera: Mymaridae) in the Neotropical region, with description of eleven new species. Zootaxa 2456: 1–243.

Ulenberg SA (1985) The systematics of the fig wasp parasites of the genus *Apocrypta* Coquerel. North Holland, Amsterdam, 173 pp.

Vilhelmsen L (2000) The ovipositor apparatus of basal Hymenoptera (Insecta): phylogenetic implications and functional morphology. Zoologica Scripta 29(4): 319–345. https://doi.org/10.1046/j.1463-6409.2000.00046.x

Vilhelmsen L (2003) Flexible ovipositor sheaths in parasitoid Hymenoptera (Insecta), Arthropod Structure and Development 32(2/3): 277–287. https://doi.org/10.1016/S1467-8039(03)00045-8

Vilhelmsen L, Isidoro N, Romani R, Basibuyuk HH, Quicke DLJ (2001) Host location and oviposition in a basal group of parasitic wasps: the subgenual organ, ovipositor apparatus and associated structures in the Orussidae (Hymenoptera, Insecta). Zoomorphology 121: 63–84. https://doi.org/10.1007/s004350100046

Vilhelmsen L, Mikó I, Krogmann L (2010) Beyond the wasp-waist: Structural diversity and phylogenetic significance of the mesosoma in apocritan wasps (Insecta: Hymenoptera). Zoological Journal of the Linnean Society 159: 22–194. https://doi.org/10.1111/j.1096-3642.2009.00576.x

Vilhelmsen L, Turrisi GF (2011) Per arborem ad astra: Morphological adaptations to exploiting the woody habitat in the early evolution of Hymenoptera. Arthropod Structure and Development 40: 2–20. https://doi.org/10.1016/j.asd.2010.10.001

Wiebes JT (1966) The structure of the ovipositing organs as a tribal character in the Indo-Australian sycophagine Torymidae (Hymenoptera, Chalcidoidea). Zoologische Mededelingen 41: 151–159.